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Stimulus luminance and the spatial acuity of domestic fowl (*Gallus g. domesticus*)

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ABSTRACT

The luminance dependence of spatial acuity in domestic fowl was measured directly over stimulus luminances ranging from 0.06 to 57.35 cd m^{-2}. At the highest luminance, acuity was around 6.5 c deg^{-1}, in agreement with previous studies in this species. As stimulus luminance decreased, acuity fell with increasing rate to 3.2 c deg^{-1} at 0.06 cd m^{-2}, following the same shape as acuity functions for other mammalian and avian species. These findings suggest that the rod–cone transition for domestic fowl is between 0.45 and 1.79 cd m^{-2}. Over the photopic range from 1.79 to 57.35 cd m^{-2} the change of acuity for fowl was 1%, compared with 32% for humans. For domestic fowl, the Rovamo–Barten MTF model of contrast sensitivity accounted for the behaviour of acuity as a function of luminance down to mesopic levels.

1. Introduction

Domestic fowl (*Gallus gallus domesticus*) are used as an animal model in biomedical research as well as being an important food source worldwide. Most fowl are reared indoors where the luminance, spectral composition and flicker characteristics of the light environment differ greatly from the natural environment in which their ancestors evolved (Prescott, Jarvis, & Wathes, 2004; Prescott & Wathes, 1999a; Prescott, Wathes, & Jarvis, 2003). Vision is considered the dominant sense in most avian species (Appleby, Mench, & Hughes, 2004) and the unnatural light environment of commercial farming can affect social and other behaviours – and hence the welfare – of domestic fowl.

All three basic visual processes (spectral, temporal and spatial) have previously been quantified for domestic fowl. The spectral sensitivity of domestic fowl has been measured using a psychophysical method, and its consequences for the calculation of luminous flux have been determined (Prescott & Wathes, 1999b; Saunders, Jarvis, & Wathes, 2008). Opponent mechanisms underlying colour vision have also been proposed (Osorio, Vorobyev, & Jones, 1999). The flicker sensitivity of domestic fowl has also been measured psychophysically and a mechanistic model of temporal vision has been formulated using these data (Jarvis, Taylor, Prescott, Meeks, & Wathes, 2002). Within the spatial domain of vision, the minimum separable acuity of domestic fowl has been measured by various methods; a psychophysical Y-maze method yielded an acuity of 1.5 c deg^{-1} in chicks, aged from 1 to 25 days old (Over & Moore, 1981), a psychophysical operant task with hens (age unspecified) provided a value of 4–6 c deg^{-1} (DeMello, Foster, & Temple, 1992) and an optokinetic nystagmus paradigm (head tracking movements indicating that a stimulus rotating around the bird is perceived) with 8 day-old chicks yielded 7.7–8.6 c deg^{-1} (Schmid & Wildsoet, 1998). These values were all measured under photopic conditions but provide a wide range of estimates of acuity, possibly due to different experimental conditions and techniques, as well as the range in age of the birds used. The contrast sensitivity function (CSF) has recently been quantified for adult laying hens using an operant task (Jarvis, Abeyesinghe, McMahon, & Wathes, 2009); this method describes the spatial visual abilities more fully than allowed by measurements of acuity. The CSF was shown to be much lower than that of humans at all spatial frequencies, with the peak of the function at approximately 1 c deg^{-1} and an acuity of about 7 c deg^{-1} under photopic conditions (at a stimulus luminance of 16 cd m^{-2}). In mammalian, fish and some avian species, spatial contrast sensitivity and acuity are known to decrease as stimulus luminance decreases, but the responses of most avian, and indeed mammalian and fish, species are not known. To provide a preliminary estimate of the response to stimulus luminance in domestic fowl, the CSF was also measured at 0.1 cd m^{-2}, which, when extrapolated to high contrast stimuli, provided an acuity measurement of about 5 c deg^{-1} (Jarvis et al., 2009). However, the luminance-dependence of spatial vision in domestic fowl has not been investigated comprehensively.

Understanding of the luminance-dependence of spatial vision in domestic fowl provides essential information on how the visual system of this – and potentially other avian – species functions under scotopic, mesopic and photopic conditions. This has direct relevance to animal welfare, as in poultry farming illuminance is commonly reduced to 5 lux or less (Prescott et al., 2003) to control

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outbreaks and prevent the recurrence of injurious feather pecking and cannibalism. Five lux corresponds to mesopic viewing conditions in the human, but it is unknown what viewing conditions it corresponds to in domestic fowl. This husbandry practice may impede the ability of domestic fowl to discriminate between one another, thereby inhibiting the maintenance of peck-orders that can be well defined and are thought to be important in their social behaviour (Rushen, 1982; Williams & McGibbon, 1956). Measurements of the CSF at a low luminance by Jarvis et al. (2009), equivalent to an illuminance at the pecking key of 0.02 lux, inform us of the visual ability of domestic fowl, but not over a range of illuminance including scotopic, mesopic and photopic conditions.

In humans, the transition from cone- to rod-dominated vision causes a marked change in acuity. This rod–cone transition has been well demonstrated in mice with rod-only phenotype and cone-only phenotype populations compared against a wild-type strain (Umino, Solessio, & Barlow, 2008), although the transition was not derived from acuity but peak contrast sensitivity. In pigeons, the transition between cone- and rod- dominated vision occurs after about 20 min of dark adaptation (Blough, 1955, 1956). The luminance level identifying this break in pigeons is about 1 cd m^{-2} (Ghim, 1997; Hodos & Leibowitz, 1977; Hodos, Leibowitz, & Bonbright, 1976), however has not been identified in any other diurnal avian species. Pigeons showed a 60% decrease in acuity as retinal illuminance decreased from approximately 2400–46 Trolands, Td (Ghim, 1997). As spatial vision of pigeons and domestic fowl is based on analogous physiological and anatomical mechanisms (Jarvis & Wathes, 2007), a similar reduction in acuity should be expected in domestic fowl. Pigeon acuity appeared to decrease at a steady rate as luminance decreased, not demonstrating the expected increase in gradient of the acuity-luminance function with the rod–cone transition (Ghim, 1997). The lack of apparent rod–cone transition in these data may be due to an inadequate luminance range; a plateau in the acuity-luminance function whereby acuity is at a maximum that is not apparent at higher luminances and the lower luminances may not have provided conditions where vision is rod-dominated in pigeons.

It is now known that the vertebrate CSF can be simulated accurately with a modulation transfer function (MTF) model (Jarvis & Wathes, 2007, 2008). This model is based on that outlined for human vision by Barten (1999), Rovamo, Kankaanpaa, and Kukkonen (1999), Rovamo, Luntinen, and Nasanen (1993), Rovamo, Mustonen, and Nasanen (1994) and is given by:

$$\mathrm{CSF}(u,I) = K \cdot O(u) \cdot H(u) \cdot A(u) \cdot [N(u,I)]^{-0.5} \quad (1)$$

where u and I represent spatial frequency in c deg^{-1} and retinal illuminance in Td, respectively. Functions O, H and A are MTFs associated with different parts of the visual system. Function O is associated with the optics of the eye and receptor sampling, function H represents lateral inhibition in the retina and A represents spatial integration. Function N represents the combination of neural and photon noise in the visual system. The term K is a cortical detection factor. This model, including full mathematical descriptions of O, H, A, N and K, together with the methods used to evaluate numerical values for their parameters are given elsewhere (Jarvis & Wathes, 2007, 2008). This model has been applied to spatial vision of domestic fowl and shown to adequately predict the CSF (Jarvis et al., 2009), thereby providing a tool that can be used to predict spatial visual abilities of domestic fowl under photopic conditions.

The aims of this study were to investigate the visual acuity of domestic fowl as a function of luminance down to scotopic conditions and to compare the results with human acuity measured under similar conditions. A key hypothesis to be tested was that the gradient of the acuity-luminance function of domestic fowl would reveal a luminance level similar to that found in pigeons of about 1 cd m^{-2} for the rod–cone transition in vision.

2. Materials and methods

2.1. Subjects

Sixteen domestic fowl of a commercial laying strain (obtained at point-of-lay, age 16 weeks Hyline Brown; Noble Foods Ltd., UK) were housed under natural light in an outdoor paddock with access to shelter. Prior to acquisition, the fowl were reared from day-old on litter under commercial conditions. The fowl had *ad libitum* access to water, grit and commercial layer pellets. Six human volunteers, two emmetropic, and the others wearing corrective lenses to compensate for any myopia, were selected from volunteers with a mean ± standard error age of 24.2 ± 1.14 years for the human comparison. Only one subject had prior experience as a psychophysical subject.

2.2. Operant apparatus, stimulus presentation and control

The apparatus consisted of an instrumented cage controlled by a PC. On one side of the cage were two transparent, pecking keys (Perspex, each 125 by 110 mm, positioned 340 mm from the floor of the cage and separated by 130 mm). The keys were hinged at the top and movement of the key was registered as a peck response by a linked PC via a circuit break. A small food trough was located between the keys and 270 mm from the floor of the cage. Blue bottle maggots, bought from a local angling shop, then frozen for storage and boiled when required were delivered to this trough by a motorised conveyor belt that could be controlled either manually or by the PC.

The stimuli were presented on two monitors (AL1511; Acer, Taiwan), placed 400 mm behind the pecking keys, viewed through them and controlled by the same PC system that controlled the instrumented cage. The output of each monitor was balanced to provide the same luminance using a calibrated luminance meter (LS-110; Minolta Camera Co., Osaka, Japan). Achromatic, vertical sine wave gratings of between 20 and 210 cycles across the width of the monitor with Michelson contrasts of 0.94 were generated and presented on either of the monitors with bespoke software. Plain grey images of the mean luminance of the sine wave grating stimuli could also be generated and were presented simultaneously with the corresponding grating stimuli. Neutral density filters (combinations of 0.3, 0.6, 0.9 and 1.2 ND, product numbers 209, 210, 211 and 299, respectively, Lee Filters, Andover, UK) were placed immediately behind the pecking keys in order to reduce the luminance of the stimuli. For the human comparison, only one monitor was used at a viewing distance of 5400 mm in order to present stimuli of high enough frequency to cover the expected range of human acuity (50–60 c deg^{-1}). Human subjects wore blacked-out, safety goggles fitted with neutral density filters to reduce the light flux reaching the eye.

Acuity was measured at eight mean stimuli luminances, ranging between 0.06 and 57.35 cd m^{-2}. A lux meter (Testo 545, Testo Ltd., Germany) was used to measure illuminance from the point domestic fowl viewed the stimuli, illuminance ranged from less than 1–52 lux. Using measurements of the pupil size (Barbur, Prescott, Douglas, Jarvis, & Wathes, 2002) and posterior nodal distance (PND; Jarvis, Prescott, & Wathes, 2003) of domestic fowl, retinal illuminance was estimated to be between 8.84 and 5060 Td. For the human study, six luminances (0.01, 0.05, 0.11, 3.47, 13.87 and 62.00 cd m^{-2}) were chosen, ranging from photopic to the upper limit of scotopic viewing conditions; these were similar to a subset of those used in the fowl study. The equivalent retinal

illuminance for humans ranged from 0.38 to 484.69 Td. This large difference in range between human and domestic fowl retinal illuminance is due not only to the difference in range of stimulus luminance, but also to the differences in pupil size and PND; the eyes of domestic fowl have a relatively small *f*/number (Schaeffel, Howland, & Farkas, 1986), therefore relatively small changes in pupil size have a greater effect on retinal illuminance in their smaller eyes.

2.3. Experimental method

The fowl were trained using a conventional shaping procedure. Each was trained to peck at the pecking keys (with grating stimulus displayed behind) in order to obtain a small food reward of a single maggot. Maggots are highly palatable to domestic fowl, which are highly motivated to 'work' for them (Bruce, Prescott, & Wathes, 2003). Pecking the control 'grey' key did not result in a food reward. Each subject was trained in a daily session comprising up to 40 trials. Training continued until a fixed ratio response of three had been reached, i.e. within a trial the subject pecked three times on the panel showing the grating and never pecked on the panel showing the uniform stimulus. The success criterion to progress was at least 80% correct choices.

For each fowl, reliable threshold measurements were taken only once the fowl's eye had become adapted for a period of at least 30 min to the luminance being tested. For each fowl, the threshold spatial frequency for each of the three lowest stimulus luminances (0.06, 0.11 and 0.45 cd m^{-2}) was determined using a stepwise approximation method based on that used by Jarvis et al. (2009). The criteria for a successful discrimination were that either the subject made consecutive correct choices (i.e. pecked at the key behind which the sine wave grating was displayed and was subsequently rewarded) over three changes in stimulus position or it made the correct choice in eight out of 10 consecutive trials. The three consecutive positional changes criterion was selected due to the potential time saving advantages and an increase of less than 4% in false positive rate compared to the method of constant stimuli more commonly used in this type of study (for example, Fite, 1973; Hodos & Leibowitz, 1977; Hodos et al., 1976; Pasternak & Merigan, 1981). The criterion of eight out of 10 trials correct was required as a further time saving measure if the three positional changes criterion failed. In addition, apparent frustration or disinterest (identified as when a fowl did not peck a key within one minute after the opaque door was raised) was used as evidence of unsuccessful discrimination. Behaviours associated with this were repeated escape attempts, resting at the back of the chamber, foraging or nesting related behaviour and stimulus observation without approach. The number of tests for each subject depended on how long it took to reach the threshold spatial frequency. Repeated measurements were taken for the highest two luminances to control for any learning effect.

At the five highest stimulus luminances (1.79–57.35 cd m^{-2}), the grating stimulus produced by the monitors was aliased at the spatial frequencies required and therefore a different approach was required. For each of these luminances, the CSF was determined at four fixed grating frequencies (0.64, 1.92, 3.84 and 5.75 c deg^{-1}) by varying the modulation depth in a stepwise approximation method as detailed above. Once these measurements had been made, acuity was estimated using the Rovamo–Barten model of contrast sensitivity (Jarvis et al., 2009) to extrapolate the measured CSF to a contrast sensitivity of 1 (equivalent to a modulation depth of 100%).

To facilitate the learning of the key-peck response, the fowls' heads were not restrained, so a single viewing distance was not defined. The viewing distances used by the hens were determined using a video camera mounted above the pecking keys, as well as measurements of the beak-tip to nostril distance to provide a scale. All hens were observed to use a final viewing distance of approximately 500 mm, which meant the spatial frequencies of the stimuli covered the range 0.61–7.76 c deg^{-1}.

Each of the human subjects was presented with the same grating stimuli as the fowl, but without the paired mean grey image and asked to respond verbally as to whether or not they could perceive the grating. The same simultaneous stimulus presentation task as used with the domestic fowl subjects was not possible with the human subjects for practical reasons caused by the long viewing distance required. However, in an investigation of human contrast sensitivity determined from a number of studies including both simultaneous and successive stimulus presentation methods, Barten (1999) found no significant variation in model parameter values between the two stimulus presentation methods, indicating that both methods produce comparable results. In addition, in a recent study of flicker sensitivity of domestic fowl that directly compared threshold measurements between the two stimulus presentation methods, both produced similar threshold measurements (Railton, Foster, & Temple, 2008). The spatial frequency was lowered in large steps until the subject could no longer see the grating stimuli, then increased or decreased by small amounts as required until the subject could only just see the grating. Each subject was asked to repeat the procedure for each luminance and was adapted to the luminance conditions for 15 min before each measurement. This dark adaptation time is half that used for domestic fowl, however, falls on the same point on the dark adaptation curve (Blough, 1955, 1956; Normann & Werblin, 1974; Rushton, 1961). The modified goggles were worn by the subject during the adaptation period and during measurements when required.

3. Results

Seven of the 16 fowl learnt the discrimination task, and of these, six learnt the stimulus generalisation and were used to obtain threshold measurements of acuity. Explanations for failure of a subpopulation to achieve task–performance include those unrelated to visual capacity; e.g. a lack of reward motivation competing behavioural motivation (e.g. nesting, fear, frustration), or an inability to learn the task. One bird was not able to generalise the operant task to lower luminances and so provided measurements at only 57.35 cd m^{-2}. As the CSF, and therefore acuity, was observed to remain constant over the range 1.79–57.35 cd m^{-2}, only three birds were used to obtain threshold acuity at 3.58, 14.33 and 28.67 cd m^{-2}. At the lowest luminance, 0.06 cd m^{-2}, only two birds performed the operant task; the other three were observed to remain quiet and exhibit some roosting behaviour. No fowl would perform the task at luminances dimmer than 0.06 cd m^{-2}.

Fig. 1 shows the mean CSF (mean ±1 standard error) at four frequencies for all fowl averaged over the five highest luminances (1.79–57.35 cd m^{-2}) at which the CSF was measured; the predicted CSF from the Rovamo–Barten MTF model is also shown (solid curve). Manually adjusting parameter values based on Jarvis et al. (2009) to fit the Rovamo–Barten MTF model to the CSF data gave a peak sensitivity at about 1 c deg^{-1} and an acuity of about 6.5 c deg^{-1}. There was very little variance in the CSFs between birds or luminance over this range.

The mean acuity (±1 standard error) of humans and domestic fowl (filled symbols with solid line and open symbols with dashed line, respectively) are shown in Fig. 2, as a function of stimulus luminance. Acuity predicted by the Rovamo–Barten model is also shown for both of these species. Domestic fowl had a much lower visual acuity than humans at all luminances; the maximum acuity was about 6.5 c deg^{-1} at 1.79 cd m^{-2} and above and fell to

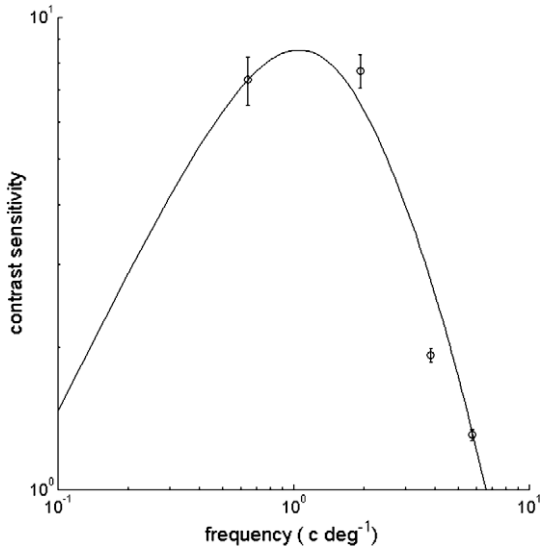

Fig. 1. Contrast sensitivity averaged over five luminances (1.79–57.35 cd m^{-2}) and five subjects for the domestic fowl (symbols ±1 standard error) and contrast sensitivity predicted by the Rovamo–Barten MTF-based model (curve).

3.2 c deg^{-1} at 0.06 cd m^{-2}. For domestic fowl, the rod–cone transition appeared to occur at a luminance between 0.45 and 1.79 cd m^{-2}. Overall, the acuity function follows the same shape as that measured in other species; a constant maximum acuity of 6.5 c deg^{-1} under photopic conditions at 1.79 cd m^{-2} and above, then a slope of increasing gradient as luminance decreases below this. A constant acuity under expected rod-dominated viewing conditions was not found. The measurements of human acuity followed the same shape as predicted by the Rovamo–Barten model and those found by previous researchers (for example, Ghim, 1997; Pasternak & Merigan, 1981; Shlaer, 1937; van Meeteren & Vos, 1972). Over the photopic range 1.79–57.35 cd m^{-2} the change in acuity for domestic fowl was 1%, compared with 32% for humans; however, when plotted as a function of retinal illuminance (Fig. 3; relative acuity, acuity scaled as a percentage of the maximum, is plotted in order to make the comparison clearer), this difference was not so apparent.

4. Discussion

To the best of our knowledge, these findings are the most comprehensive measurements of the effects of stimulus luminance on spatial acuity of a domestic poultry species. At a stimulus luminance of 0.06 cd m^{-2}, only two birds performed the operant task: below this luminance, no birds would work at all. This correlates with an observation from a pilot study that domestic fowl spent less time foraging for maggots at decreasing illuminance. At this luminance, the subjects remained quiet or sought a perch, indicating that they had a greater motivation to roost than to work for an extremely palatable food reward. This was probably due to the long adaption period the birds experienced prior to entering the operant chamber: the dim light is likely to have induced drowsiness or sleep. Under these circumstances, behavioural measures of visual ability were unobtainable.

The CSFs of domestic fowl measured under photopic conditions in this study match closely those found by Jarvis et al. (2009) and correlate well with other measurements of acuity in this species (DeMello et al., 1992; Schmid & Wildsoet, 1998). With the repeatability of the behavioural measurements of CSF and acuity observed over a range of stimulus luminances in the photopic range, a value of about 6.5 c deg^{-1} for maximum acuity of domestic fowl seems plausible.

Measured acuity as a function of luminance in domestic fowl closely matched the relationship predicted by the Rovamo–Barten model as well as that found in other species including humans. This indicates that the same mechanisms that underlie spatial vi-

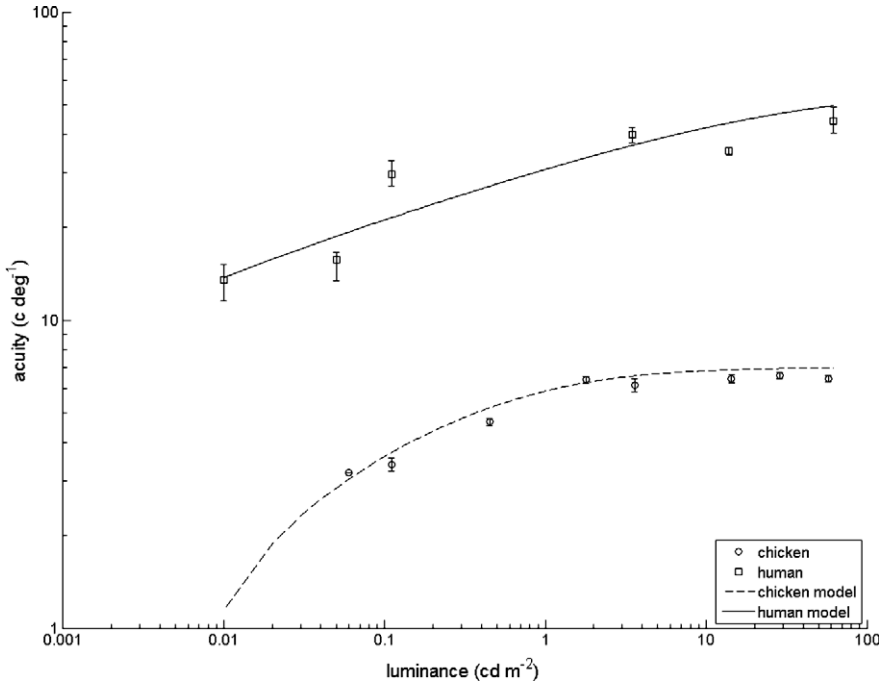

Fig. 2. Mean acuity (c deg^{-1}) as a function of luminance (cd m^{-2}) measured for the domestic fowl (open circles) and human (filled circles) and modelled for the domestic fowl (broken line) and human (solid line). All error bars are ±1 standard error; some error bars are obscured by the symbols. Sample sizes for the measured fowl data are $n = 5$ at 0.11, 0.45, 1.79 and 57.35 cd m^{-2}, $n = 3$ at 3.58, 14.33 and 28.67 cd m^{-2} and $n = 2$ at 0.06 cd m^{-2}. Sample sizes for the measured human data are $n = 5$ at 0.01 cd m^{-2} and $n = 6$ at all other luminances.

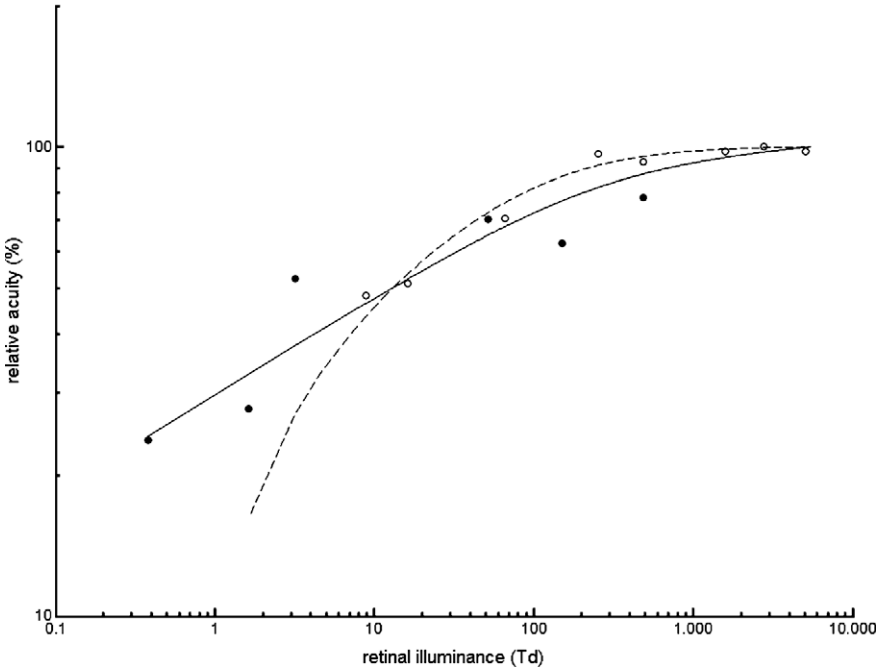

Fig. 3. Acuity scaled as a percentage of the maximum against retinal illuminance (Td). Measured average data for the domestic fowl and human are represented by open and filled circles, respectively, and curves modelled from the Rovamo–Barten MTF-based model for the fowl and human are represented by broken and solid lines, respectively. Error bars are omitted for clarity.

sion at low luminances in other vertebrates also act in domestic fowl, further supporting the use of the Rovamo–Barten MTF-based model of spatial vision in a range of vertebrates including birds (Jarvis & Wathes, 2008). The magnitude of acuity of domestic fowl also closely matched that predicted by the Rovamo–Barten model over the range of stimulus luminances measured, further supporting the use of this model. Although the Rovamo–Barten model was derived for photopic vision, it also fitted the acuity of domestic fowl at luminances where rod vision becomes important. This may indicate that the model is applicable to scotopic conditions. Conversely, an alternative explanation would be that the behavioural tendencies of domestic fowl to roost at lower luminances did not allow acuity to be measured under true scotopic conditions and the lowest luminances measured are, in fact, still mesopic conditions for domestic fowl. Mesopic vision allows some contribution from the cone photoreceptors, and therefore the photopic MTF model appears to adequately describe the acuity function to these luminances, even though it has not been adjusted to take into account the difference between rod- and cone-dominated vision.

A further explanation of why clear scotopic vision was not observed could be that there is a strong diurnal control of rod function during the day; Schaeffel, Rohrer, Lemmer, and Zrenner (1991) found no evidence of rod function in electroretinograms (ERGs) of domestic fowl during the daytime, regardless of up to 24 h dark adaptation time, however were able to demonstrate rod function between midnight and 3.00 am. Japanese quail kept in constant darkness demonstrated increased photoreceptor responses in ERGs during the subjective night (Manglapus, Uchiyama, Buelow, & Barlow, 1998). The spectral sensitivity measured with the photoreceptor responses matched the sensitivity of rhodopsin at night, but not during the day, indicating suppression of rod function during the day, mediated by dopamine (Manglapus, Iuvone, Underwood, Pierce, & Barlow, 1999). Our threshold measurements were made between 9.00 am and 4.00 pm, only those threshold measurements gained towards the end of this period could have possibly have had any contribution from the rod cones. As a result, the acuity data at lower stimulus luminances may not be a true representation of the mesopic or scotopic visual abilities of domestic fowl and further work is required to establish this, however this does not affect the findings for cone-dominated vision.

Over the range of stimulus luminance which acuity was measured for humans, the change in gradient caused by the rod–cone transition was not apparent, as it was in domestic fowl over the same range. This is expected, as the Rovamo–Barten MTF model and results from Shlaer (1937) predict that the acuity function for humans has a rod–cone transition centred at 0.01 cd m^{-2} and maximum acuity under photopic conditions is reached at about 50 cd m^{-2}, the respective lower and upper limits of the range used here. Due to this, the range 0.01–62 cd m^{-2} only provides a description of acuity over the upper part of mesopic viewing conditions for humans, and there will not be much apparent change in gradient of the acuity function.

Our results suggest that the rod–cone transition in domestic fowl occurs between 0.45 and 1.79 cd m^{-2}. This is much brighter than the comparable value of between 10^{-4} and 0.01 cd m^{-2} for mice (Umino et al., 2008), about 0.01 cd m^{-2} for humans (calculated from Shlaer, 1937), between 0.1 and 1.1 cd m^{-2} for owl monkeys (Jacobs, 1977) and about 0.16 cd m^{-2} for cats (Pasternak & Merigan, 1981). The rod–cone transition occurs for pigeons at about 1 cd m^{-2} (Fig. 4, Ghim, 1997; Hodos & Leibowitz, 1977; Hodos et al., 1976) which is very similar to the value we found for domestic fowl, proving the hypothesis that domestic fowl and pigeons would exhibit similar visual abilities.

Fig. 4 shows acuity as a function of luminance for a variety of species; humans and domestic fowl from this study, cat (Pasternak & Merigan, 1981), owl monkey (Jacobs, 1977) great horned owl (Fite, 1973) and pigeon (Ghim, 1997; Hodos & Leibowitz, 1977; Hodos et al., 1976). The acuity-luminance function for the cat used in this analysis is scaled up by a factor of 1.8 from the data published by Pasternak and Merigan. This is because the human acuity-luminance function from the Pasternak and Merigan study (not included in Fig. 4), although the expected shape, had magnitudes 1.8 times lower than found in this and other studies (for

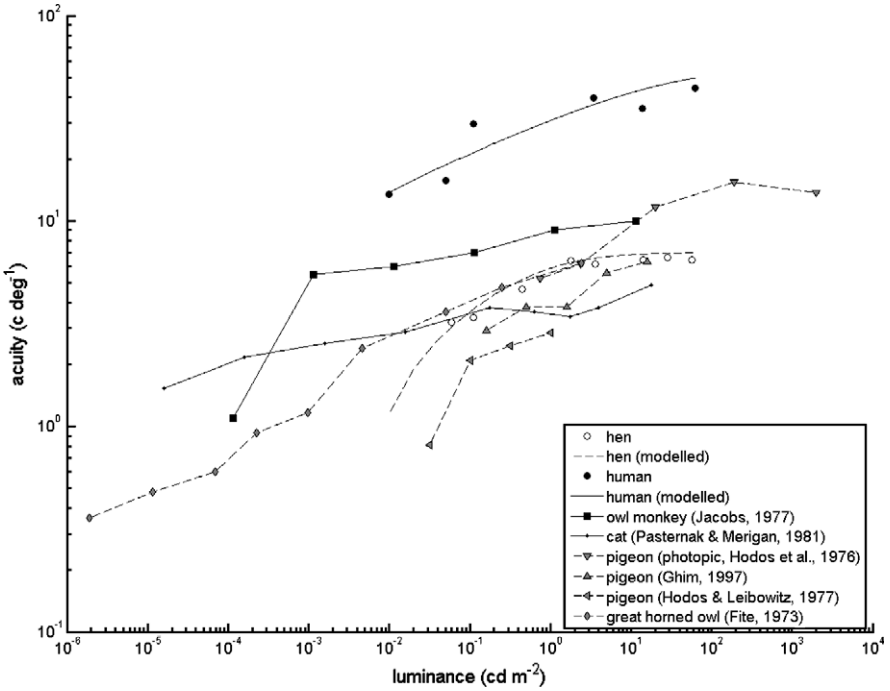

Fig. 4. Mean acuity (c deg^{-1}) as a function of stimulus luminance (cd m^{-2}) for the domestic fowl (white circles), human (large black circles), owl monkey (black squares, Jacobs, 1977), cat (small black circles, Pasternak & Merigan, 1981), great horned owl (grey diamonds, Fite, 1973) and pigeon (grey triangles, Ghim, 1997; Hodos & Leibowitz, 1977; Hodos et al., 1976). For the human and the fowl, symbols represent measured data and the curves show the Rovamo–Barten MTF model predictions. Continuous lines represent data from mammals, broken lines represent birds. Error bars are omitted for clarity.

example, van Meeteren & Vos, 1972). This could be due to a difference in the stimulus or procedure used by Pasternak and Merigan compared to other studies. As the cat and human subjects were both tested with the same stimuli under the same conditions it is likely that the cat data are also underestimates of the true values and require scaling before they can be used in an inter-species comparison.

Over the photopic range 1.79–57.35 cd m^{-2}, our experiment shows that the change of acuity for domestic fowl was 1%, compared with 32% for the human. Also, pigeon acuity decreased by about 54% over the same range (Hodos et al., 1976), however, in domestic fowl, there was only a decrease of 29%. Maintenance of acuity as luminance decreases similar to that found in domestic fowl is apparent in a nocturnal avian species, the great horned owl as well as two nocturnal mammalian species, cats and owl monkeys, suggesting an adaptation in domestic fowl to dim lighting conditions. This adaptation could be vestigial from the progenitor species of domestic fowl, red jungle fowl (*Gallus gallus*), which is crepuscular and inhabits the margins of the jungle.

An environmental illuminance of 5 lux is equal to a stimulus luminance of about 5.51 cd m^{-2} under these experimental conditions. At this luminance, acuity is still at its maximum so there should be no decrease in spatial visual ability for domestic fowl under the typical agricultural conditions of the poultry house. However, due to the spectral or flicker characteristics of the light sources used, there still could be some impairment of overall visual ability of domestic fowl under these conditions. The acuity of domestic fowl as a function of retinal illuminance varies in a similar manner to humans (Fig. 3). This may be related to the relatively small change in the optical performance in domestic fowl for the range of pupil sizes encountered in varying stimulus luminance from 1.79 to 57.35 cd m^{-2}. The pupil diameters encountered under these luminances in domestic fowl are 5.2 and 4.1 mm, respectively (Barbur et al., 2002) and the change in optical performance over a similar change in pupil size is relatively small (Coletta, Marcos, Wildsoet, & Troilo, 2003). A mechanism related to this is how pupil diameter influences retinal illuminance in relatively small eyes; a small change in pupil size will have a greater effect on retinal illuminance in small eyes compared to the same change in pupil diameter in large eyes. Therefore, domestic fowl will be able to maintain retinal illuminance as stimulus luminance decreases with smaller increases in pupil diameter than would be observed in humans. The optical performance of the lens of the vertebrate eye decreases towards the edges. Therefore, the smaller increase in pupil size found in domestic fowl prevents decreases in optical performance.

In summary, the acuity of domestic fowl demonstrates the same behaviour over a range of stimulus luminances as other vertebrates and as predicted by current MTF-based models. The spatial visual ability of domestic fowl is less subject to change than human and pigeon spatial visual ability over a practical range of 1.79–57.35 cd m^{-2} (approximately 2–52 lux), due in part to a lower decrease in optical performance of domestic fowl over this range, but also subject to neural noise and retinal integration factors.

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